

# A mosaic pattern characterizes the evolution of the avian brain

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**Diversity in vertebrate brain size and composition is thought to arise from either developmental constraints that cause coordinated changes between brain regions or a mosaic model, whereby changes in individual brain regions are independent of changes in other brain regions. These two mechanisms were tested in birds using multiple regression analyses. Across 13 orders, significant correlations were present between some brain regions, but not all. Most of the correlated changes reflect the connectivity between different brain components, such that regions with the most interconnections are correlated with one another but not other brain regions. Whether mosaic changes are characteristic of brain regions or systems in birds, however, to our knowledge, remains to be investigated.**

**Keywords:** brain structure; birds; correlated evolution

## 1. INTRODUCTION

The brain is a heterogeneous organ composed of multiple regions that are functionally specific. The importance of these distinct regions in mediating specific behaviours means that they are subject to similar evolutionary selection pressures to those acting on the behaviours (but see Bolhuis & Macphail 2001). As a result, there is great diversity in relative brain size and composition between species and correlations are frequently drawn between this neural diversity and the behaviours that they mediate. However, brain regions do not evolve in isolation since they are interconnected with other regions as part of functional circuits and systems. In fact, comparative studies of neural systems indicate that correlated changes do occur between functionally connected regions (Barton *et al.* 1995; Barton & Harvey 2000; Whiting & Barton 2003). Two opposing, but not exclusive, theories have been proposed to explain these correlated changes.

The first theory proposes that developmental constraints cause coordinated changes in size between brain regions (Finlay & Darlington 1995; Finlay *et al.* 2001). The result of these changes is that relatively large brains are 'scaled-up' versions of smaller brains, with similar proportions of different brain regions. This is primarily because of differences in the timing of peak neurogenesis affecting overall brain size. The 'developmental

constraints theory' has, however, been dismissed as an inadequate sole explanation for species differences in brain region size and architecture (Barton 2001; Kaas & Collins 2001; Marino 2001; Striedter 2001).

The second theory suggests that overall brain size can be increased by the expansion of specific brain regions independently of other regions (Barton & Harvey 2000; de Winter & Oxnard 2001; Rehkamper *et al.* 2001; Barton *et al.* 2003; Whiting & Barton 2003). Several examples of this are provided in Rehkamper *et al.* (2001) and include greater expansion of olfactory, spatial and somatosensory regions than of other brain regions. The 'mosaic theory' has been corroborated by multivariate analyses (Barton *et al.* 2003; Whiting & Barton 2003), which demonstrate that not only do mosaic changes occur, but the relative proportions of brain regions are order-specific (Barton & Harvey 2000; de Winter & Oxnard 2001). That is, there are differences between orders and species in the structural organization of the brain and these are, in turn, representative of ecological differences.

As with most theories regarding the evolution of brain size and structure differences, most of the evidence to date has focused on mammals. Whether similar mechanisms also operate in brain size and structure diversification in other vertebrates has therefore remained untested. Using data from both the literature and measurements taken from serially sectioned brains, we tested whether these competing theories can explain interspecific differences in avian brain structure. If the developmental constraints theory represents the primary mechanism, then we expected that changes in the size of one brain structure would be correlated with changes in all other brain structures. If, however, the mosaic theory is the predominant mechanism, then we expected that changes in one brain region would occur independently of other brain regions. Based upon the analyses presented in mammals, any significant correlations are likely to be between those regions sharing the greatest interconnectivity (Barton & Harvey 2000). Specifically, we expected significant correlations between five region pairs because of the large number of connections that they share with one another: telencephalon and diencephalon; diencephalon and mesencephalon; mesencephalon and optic tectum; mesencephalon and myelencephalon; and myelencephalon and cerebellum (Clarke 1977; Bravo & Pettigrew 1981; Arends & Zeigler 1991; Wild *et al.* 1993; Wild 1997; Husband & Shimizu 2002).

## 2. MATERIAL AND METHODS

### (a) Data

Volumetric measurements were taken directly from the brains of 36 species (see electronic Appendix A, available on The Royal Society's Publications Web site) that were fixed in 10% buffered formalin and dissected from bird carcasses collected from a variety of sources. Additional information on the brain composition of 25 species was taken from Boire & Baron (1994). Briefly, all of the brains were embedded in paraffin, serially sectioned in the transverse plane, mounted on gelatinized slides and stained with a modified Kluver-Barrera technique (Culling 1974). The six main regions of the brain, the telencephalon, diencephalon, mesencephalon, optic tectum, cerebellum and myelencephalon, were measured from digital photographs with NIH Image v. 1.62. Region boundaries followed the descriptions provided by Boire & Baron (1994). Volumes were then calculated by multiplying the area of each section by the sampling interval-section thickness (7 µm) and a correction factor to account for shrinkage (Stephan *et al.* 1981, 1991; Boire & Baron 1994; Baron *et al.* 1996).

### (b) Statistical analyses

Prior to performing all analyses, both region volumes and body masses were log-transformed. Following the methodology outlined in Barton & Harvey (2000), the volume of each structure was then compared with that of the other structures in multiple regressions. This is similar to calculating partial correlation coefficients for each region, but permits the forcing of regression lines through the origin for independent contrasts analysis (see below). However, Barton & Harvey (2000) did not give any details as to how, or if, body size effects were controlled in their analyses. We therefore calculated 'body-size free' residuals from least-squares linear regressions of brain region volume against body mass. The same multiple regression procedure as for the absolute volumes was subsequently applied.

To control for possible 'phylogenetic effects' we also performed the multiple-regression analyses using the independent contrasts method (Felsenstein 1985). The phylogeny used to calculate the contrasts was based upon Sibley & Ahlquist (1990), with additional resolution provided by several other sources (see Iwaniuk 2003 for details) and the calculations performed in PDPTREE, a program within the PDAP software package (available from T. Garland upon request). Since the phylogenies were taken from disparate sources, arbitrary equal and unequal branch lengths were used to test that the contrasts were adequately standardized (Garland *et al.* 1992). The multiple regressions of the independent contrasts were forced through the origin (Garland *et al.* 1992).

## 3. RESULTS

Overall, consistent correlations were only present between four brain region pairs across all four analyses: telencephalon and diencephalon; diencephalon and optic tectum; mesencephalon and optic tectum; and cerebellum and myelencephalon (figure 1*a*) (for details see electronic Appendix A). All of these were positive, so increases in the size of one region were correlated with an increase in size of the paired region.

Because the dataset was dominated by a relatively large number of psittaciforms (21/61 species), we re-analysed the data after splitting all of the species into psittaciforms and non-psittaciforms. Across the non-psittaciforms, there were four consistently significant correlations that match those described across all species (figure 1*b*; see electronic Appendix A). In addition, three of the analyses yielded a significant correlation between the mesencephalon and myelencephalon. By contrast, the analyses of the psittaciforms yielded only one consistently significant correlation: between the myelencephalon and cerebellum (figure 1*c*; see electronic Appendix A). Three of the analyses also yielded a significant correlation between the optic tectum and diencephalon. Thus, it would appear that a mosaic pattern of evolution characterizes the avian brain, regardless of what subset of species is analysed.

## 4. DISCUSSION

Overall, there was a general tendency for significant relationships to be present between adjacent regions that share substantial neuronal connections. With respect to our five specific predictions that were based upon the connectivity between regions, three of them were supported: telencephalon and diencephalon; mesencephalon and optic tectum; and myelencephalon and cerebellum. The two pairs that did not exhibit consistent significant correlations were the diencephalon and mesencephalon and mesencephalon and myelencephalon. These non-significant correlations were unexpected considering the degree of interconnectivity between the regions and that significant correlations between these regions were present in mammals (Barton & Harvey 2000; figure 2). Why

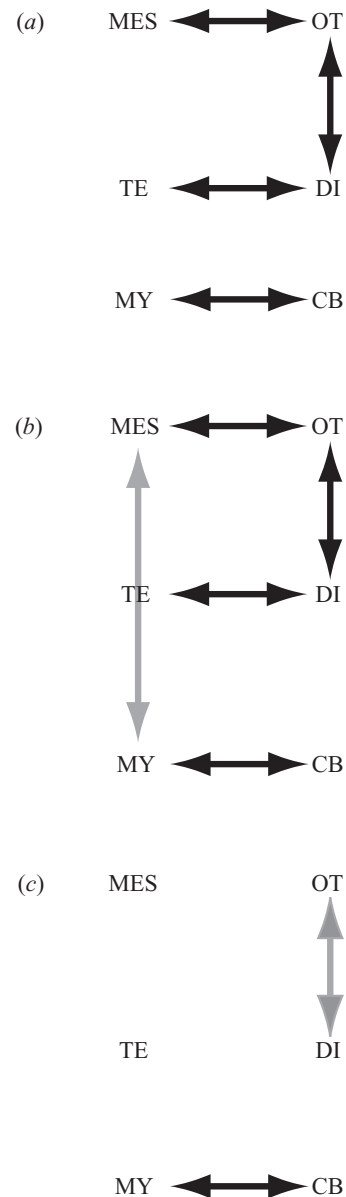


Figure 1. A graphical representation of the significant correlations between brain regions of birds is presented. The black arrows indicate that significant correlations were present across all four analyses, whereas grey arrows indicate that significant correlations were present in three of the analyses (see electronic Appendix A). The abbreviated regions are as follows: TE, telencephalon; DI, diencephalons; MES, mesencephalon; OT, optic tectum; CB, cerebellum; and MY, myelencephalon. The figures themselves refer to analyses performed across (a) all orders of birds; (b) all non-psittaciforms; and (c) the psittaciforms.

evolutionary changes in volume of these regions are not intercorrelated is uncertain at this stage, but some insight may be gleaned from similar multivariate studies at a more detailed level (e.g. correlations between sensory nuclei).

Similarly unexpected was the significant correlation between the diencephalon and optic tectum. Although not adjacent to one another, these two regions share a direct connection that passes through the mesencephalon (Bravo & Pettigrew 1981; Husband & Shimizu 2001). Although this single connection may not be the sole reason for the correlated evolution of the diencephalon and optic

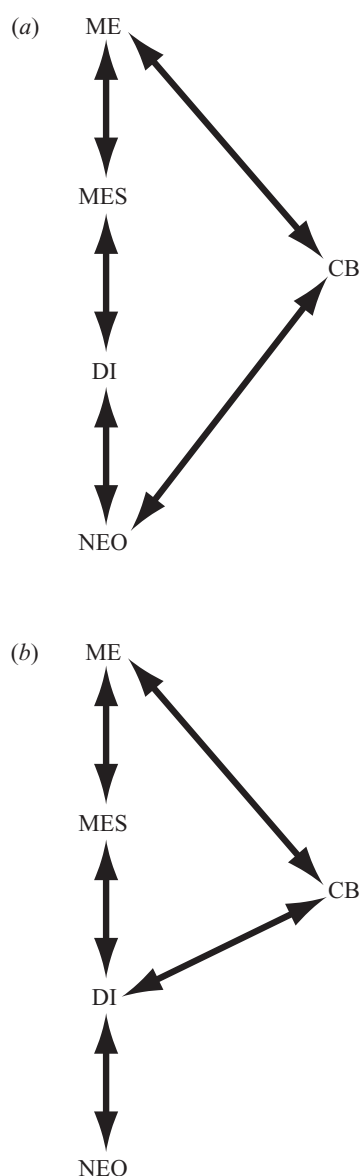


Figure 2. A graphical representation of the significant correlations between the major brain regions of: (a) primates; and (b) insectivores (adapted from Barton & Harvey 2000). The abbreviated regions are as follows: NEO, neocortex; DI, diencephalon; MES, mesencephalon; CB, cerebellum; and ME, medulla.

tectum, it may exert a significant effect on evolutionary changes in these two structures.

Why there were so few significant correlations within psittaciforms is difficult to ascertain. Furthermore, the difference between inter- and intra-order analyses may be a pattern specific to psittaciforms or it could be a more general pattern. Detailed volumetrics of brain composition within other avian orders are required to resolve this issue, but are unavailable at present.

The results of this and other studies (Barton & Harvey 2000; de Winter & Oxnard 2001; Rehkamper *et al.* 2001) demonstrate that mosaic evolution characterizes the diversification of avian and mammalian brain composition. Not only do both mammals and birds exhibit mosaic patterns of evolution, but there were few similarities between the relationships described for all birds (figure 1) and that of primates and insectivores (figure 2). The consistency of

the evidence supporting a mosaic model of evolutionary change could suggest that the developmental constraints theory does not apply to vertebrate brain evolution. On the contrary, the fact that some coordinated changes were observed suggests the operation of constraints. It is difficult to determine whether these are developmental constraints as suggested by Finlay *et al.* (2001), functional constraints or selection acting upon both structures simultaneously. Because of this uncertainty, the developmental constraints theory must remain as a viable explanation for correlated size changes between brain regions.

It is equally uncertain whether mosaic changes also occur within brain regions and/or between nuclei in birds. Correlated changes within neural circuits have been shown in mammals (Barton & Harvey 2000; Barton *et al.* 2003; Whiting & Barton 2003) and preliminary results indicate that a mosaic pattern characterizes evolutionary changes in the telencephalon of psittaciforms (Iwaniuk 2003). Similar comparisons between vocal control, auditory, visual and other nuclei may yield more insight into how widespread is the occurrence of such correlated changes in the avian brain. Exploring the correlated evolution of the vocal control system in oscines and other circuits will provide insight into their connectivity and their evolution, but will depend upon the future development of suitable comparative databases.

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